

# Social Control of Sex Change in the Bluehead Wrasse, *Thalassoma bifasciatum* (Pisces: Labridae)

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**Abstract.** While the bluehead wrasse has long been used as a test species in sex allocation theory, there is no published evidence that sex change in this species is socially controlled. Here we show that removal of large terminal color phase (TP) males from local populations leads to sex and color change in the largest initial color phase (IP) females. In contrast, no sex changes occurred in control populations in which the TP males were handled but replaced, and in which only the IP males were removed. The response to removals was quite precise, resulting in a nearly one-to-one replacement of TP males.

Large individuals that had been seen spawning as females on the day prior to the manipulation, initiated male behaviors within minutes of the removal of the TP males and spawned in the male role the same day. Color changes were noted within a day and were distinct within four days. Sex change was verified by histological examination of the gonads of the changing individuals. All had functional testes, and all showed evidence of recent transition from the ovarian condition. Mature sperm can be produced in as little as eight days after the initiation of sex change.

## Introduction

The bluehead wrasse, *Thalassoma bifasciatum*, has been the subject of intensive study in behavior and ecology for nearly 60 years (e.g., Tee-Van, 1932; Stoll, 1955; Feddern, 1965; Roede, 1972; Reinboth, 1973; Warner *et al.*, 1975; Victor, 1986, and references therein; Warner, 1988a, 1990, and references therein). The majority of individuals in this species are protogynous hermaphrodites (Warner and Robertson, 1978), and the species has served as a model against which the sex allocation theory has been

tested (Warner *et al.*, 1975; Warner and Hoffman, 1980; Charnov, 1982a,b; Warner, 1984; Hoffman *et al.*, 1985; Shapiro, 1989). An assumption made in many of these studies is that the bluehead wrasse changes sex in response to local social conditions. Here we show that *T. bifasciatum* does indeed demonstrate rather precise social control of sex change and give data as well on the time course of sex and color change.

## Background and Methods

Adult bluehead wrasses occur in two major color phases (Warner and Robertson, 1978). Smaller males and all females are in the initial color (IP) phase: a yellow dorsal stripe surmounts a lateral series of green blotches separated by white bars. The largest individuals are in the terminal color phase (TP): a bright blue head is separated from a green body by three vertical bars, two of which are black and the other white. As an individual changes from the IP to the TP phase, the head becomes suffused with blue, the two most anterior green blotches intensify, darken, and lengthen vertically, while the other blotches fade. Individuals with blue heads and green bodies, but still retaining remnants of the posterior blotches, are termed intermediate (INT). The change to TP coloration is permanent: individuals cannot temporarily revert to the IP pattern (Warner and Robertson, 1978). Both IP males and females can become TP males, the latter through sex change. Gonad anatomy can be used to distinguish TP males that are the result of sex change (termed secondary males) from those that originated as IP males (primary males; see Reinboth, 1967).

All fieldwork was carried out on patch reefs in Tague Bay, St. Croix, U. S. Virgin Islands, near the West Indies Laboratory. Manipulations of population structure on small reefs were carried out in June–August, 1989, while

the larger reef experiments were performed during the same period in 1990.

For the small reef manipulations, we chose five isolated reefs (all less than 100 m<sup>2</sup> in area) ranging in adult population size from 24 to 57 individuals. After three days of observation of mating on these reefs, all individuals were captured, sexed through examination of their genital papillae, and measured to the nearest 0.1 mm (S.L.). Females have a blunt genital papilla that protrudes over the broad genital opening, while males have a pointed papilla that terminates in a small genital aperture. In addition, sperm can always be expressed from functional males. All IP males were removed from the reefs, and on the randomly chosen experimental reefs ( $n = 3$ ) all TP and INT individuals were removed as well. On all reefs, females larger than 60 mm S.L. were tattooed with unique combinations of spots of a vital stain (Alcian Blue) before they were returned to the reef. On the control reefs ( $n = 2$ ), we removed the TP and INT males and then replaced them after 30 min. We then monitored the reproductive activity and coloration of the females on all reefs, intensively for two days after the removal, and on a weekly basis for a month thereafter. The identity of individuals showing male courtship behavior and transition to TP coloration was confirmed by noting the markings that had been applied.

Reproductive behavior was monitored during the daily mating period, which begins in the early afternoon and lasts for an average of 110 min (Warner and Hoffman, 1980). Male reproductive behavior consists primarily of aggression and courtship. Males vigorously chase all conspecifics away from the mating site, except females arriving to spawn. When a ripe female arrives, the male positions himself in the water column over the female, swimming in tight circles while rapidly vibrating his pectoral fins. He may then descend to the female and touch her dorsal area, or may swim rapidly upwards and back down in a movement reminiscent of the actual spawning rush. Females are never seen to perform these behaviors. To indicate their readiness to spawn, females will turn their head upwards, and soon after will dash upwards about a meter toward the surface, accompanied by the male. At the apex of the spawning rush, the female will flip upside down, release her eggs, and then rapidly descend.

Individuals showing evidence of sex change (that is, prior females who had initiated male behavior and coloration) were later collected. The markings and length were rechecked, and the individuals were dissected to determine gonadal state. The gonads of ten of these individuals were preserved in Bouin's solution and prepared for histological examination. Cross-sections cut at 12  $\mu$ m were stained with hematoxylin and eosin. Testicular function was verified by the presence of crypts of developing sperm. Secondary male status was indicated by the presence of a central lumen (the previously functional

ovarian cavity) into which the gonadal lamellae protrude (Reinboth, 1967; Sadovy and Shapiro, 1987). Recently sex-changed labrid fishes also have large amounts of degenerating oocytes scattered throughout the lamellae (see Warner, 1975). In contrast, primary males have a solid testis, with no evidence of either a central cavity or degenerating oocytes (Reinboth, 1967).

When the sex-changed individuals were removed from the experimental reefs, we continued to monitor the remaining residents. In addition, the TP and INT males were removed from the control reefs once the initial two-week observation period was over; subsequent monitoring ensured that the initial lack of response seen on these reefs was not due to some inherent quality of the reef itself. After the initial two-week period, we also verified sexual function of the remaining IP individuals on all reefs by capturing them before the spawning period began and holding them in nets until after spawning on nearby reefs had ended. Females who were to spawn that day could then be stripped of ripe eggs with gentle pressure applied in the dorsal area of the body cavity; on average, females spawn on two out of every three days (Warner, 1985; Schultz and Warner, 1989). Functional males express sperm under the same treatment.

Most populations of the bluehead wrasse are much larger than those present on the small patch reefs used in the experiment. To determine the precision of TP male replacement in larger populations, in 1990 we removed all TP and INT individuals from four larger reefs (300–2600 m<sup>2</sup>; total population sizes ranging between 256 and 422 individuals), and returned two weeks later to monitor the number of individuals in the remaining population that had undertaken the shift toward TP male status. Past tagging studies have shown that adults do not move from reef to reef (Warner and Hoffman, 1980; Warner, 1984, 1987), so that new TP and INT individuals could be reliably assumed to have arisen from the resident population.

## Results

### *Responses to removals of large males*

Removals were performed in the morning. On the experimental reefs, several (2–4) of the largest females present began to exhibit aggression towards other large females and to court smaller females within minutes of the removal of the large males. During the mating period that day, these same largest IP individuals (who had been observed to mate as females with a TP male on the previous day) courted and spawned in the male role with the remaining females on the reef. In contrast, on the two control reefs, the largest females spawned in normal fashion as females with the resident TP males, and continued to do so for the two-week experimental period.

Overall, there was a very strong response to the removal of TP and INT males on the experimental reefs (Table 1). Eleven such males were removed from the three experimental reefs, and nine females changed to male roles within two weeks. In contrast, no changes were noted on the control reefs over the same period, even though IP males had been removed in the same fashion as on the experimental reefs.

In every case, the individuals that undertook the shift to male function were the largest remaining individuals on the reef. Figure 1 gives an example from one of the experimental reefs. It is worth noting that the IP males tended to be located in the larger end of the IP size range, which might be expected because on small reefs they grow faster than females (Warner, 1984).

Of the 18 large IP individuals that continued to display female coloration during the initial observation period (6 on the experimental reefs and 12 on the controls), none showed evidence of male function; all continued to spawn in the female role. Fifteen of the 18 produced normal clutches of eggs on the day of capture. The remaining three had normal female genital papillae, and sperm could not be expressed from any of them.

The pattern of sex changes in response to the removal of TP and INT males continued after the initial observation period on both the experimental and control reefs (Table 1). For six subsequent removals on the experimental reefs, five females changed to the male role. The removal of 12 TP and INT individuals from the former control reefs resulted in 8 females changing to male roles, whereas

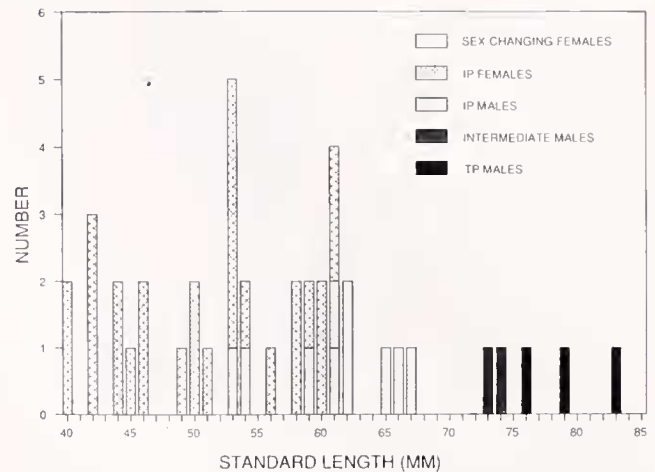


Figure 1. Beginning size, sex, and color distribution and outcome of removal of large males of *Thalassoma bifasciatum* from Reef 9A, Tague Bay, St. Croix. All males were removed, and the four largest females on the reef changed sex.

none had behaved as males before. This indicates that the control reefs contained individuals that were capable of sex change, so that the initial lack of response on these reefs was likely due to the fact that the larger males were left in residence.

The overall pattern of response for both small and larger reefs was quite precise (Fig. 2). The slope of the regression relating number changing to number removed was 0.89, which was not significantly different from a one-to-one

Table 1

Outcomes of two sets of experiments removing *Thalassoma bifasciatum* from small patch reefs in Tague Bay, St. Croix

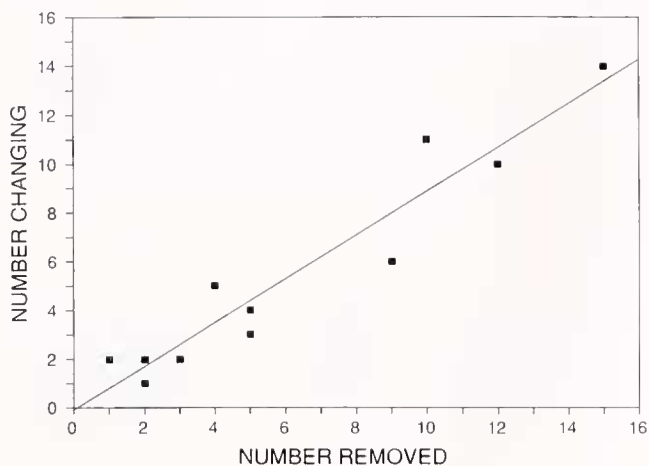
A. TP and INT removed at outset:

Reef	No. males removed			No. females remaining		No. changing sex	No. subsequent removals	No. subsequent sex changes
	TP	INT	IP	<60mm	≥60mm			
9A	3	2	6	21	6	4	2	1
9B	1	4	4	14	4	3	2	2
10	0	1	1	23	5	2	2	2

B. TP and INT remain at outset, subsequently removed:

Reef	No. males			No. females remaining		No. changing sex	No. subsequent removals	No. subsequent sex changes
	Remaining	Removed	IP	<60mm	≥60mm			
12	4	5	7	38	5	0	9	6
14	3	0	4	24	7	0	3	2

TP = Terminal Phase coloration; INT = Intermediate coloration (early Terminal Phase); IP = Initial Phase coloration. In the first set (A), all males (TP, INT, and IP) were removed at the outset. In the second set (B), only IP males were removed. The seventh column shows the number of individuals having changed sex two weeks after the experiment began. At that point, in both sets of experiments, some TP and INT individuals were subsequently removed, and the responses of the remaining individuals were noted, again after a two-week interval.



**Figure 2.** Responses of remaining individuals to removals of INT and TP males of *Thalassoma bifasciatum* on patch reefs in Tague Bay, St. Croix. Shown are the results from the removals from reefs shown in Table II (initial and subsequent removals shown separately) and four larger reefs. On the vertical axis are the total number of individuals changing from IP coloration to INT coloration during a two-week period. The dotted line represents a one-for-one response. The solid line is a regression of the number changing (NC) against the number removed (NR). The regression equation is  $NC = .894NR - 0.049$ ;  $r^2 = .91$ ,  $P < 0.001$ .

response. It should be noted, however, that not all of the responses on larger reefs were necessarily sex changes, because IP males were not removed along with the TP and INT males.

#### Changes in coloration

As early as the first day of the manipulation, IP individuals sometimes slightly darkened their heads while courting and mating. These coloration differences were

not detectable outside of the mating period. By day 3, however, the largest individuals had begun the transition to TP coloration. Over the course of the observations (a maximum of 28 days), only the two or three largest individuals on each reef proceeded to develop full INT coloration, and this was apparent within five days. In the rest of the changing individuals, the head region had a permanent bluish tinge, and the two anterior lateral blotches had darkened and enlarged, but the body was not yet green. No individuals attained full TP status over the course of the experiment. None of the IP fishes on the control reefs initiated color change during the initial experimental period.

#### Sex change verified

No individual identified as a potential sex-changer had functional ovaries. All 10 gonads examined histologically were testes engaged in active sperm production (Table II). Furthermore, all of these testes were secondary (derived from previously functional ovaries), with varying amounts of degenerating oocytic material still in the gonadal lamellae.

Sex change apparently can proceed quite rapidly. Even individual 10A3, observed spawning as a female before the manipulation and captured 8 days later, was already producing tailed sperm. Of the 10 individuals investigated histologically, in only three had spermatogenesis not yet proceeded to the production of mature sperm. All of these had been first observed to display early intermediate coloration 8 to 9 days before capture.

#### Discussion

It is clear that female bluehead wrasses change sex when larger brightly colored males are removed from the local population. Social control of sex change in reef fishes was first documented two decades ago (Fishelson, 1970; Rob-

**Table II**

*Size, coloration, two estimates of time since initiation of sex change, and gonadal state for ten individuals observed to change from initial phase coloration and female behavior to male coloration and behavior over the course of the experiments*

Fish ID	Length at capture (mm S.L.)	Coloration	Days since beginning of experiment	Days since individual began to display male coloration	Histological condition of gonad
9A2	67.0	INT	19	19	Act 2°, t.s.
9A6	65.8	early INT	28	9	Act 2°, t.s.
9B1	65.2	INT	28	28	Act 2°, t.s.
9BX	63.9	early INT	28	8	Recent 2°, t.s.
9BY	55.0	early INT	28	8	Act 2°, t.s.
9BZ	55.2	early INT	28	8	Recent 2°, no t.s.
10A1	64.6	early INT	17	9	Act 2°, no t.s.
10A3	69.3	early INT	8	8	Act 2°, t.s.
10A4	65.3	early INT	17	9	Act 2°, no t.s.
T41	64.5	early INT	17	9	Act 2°, t.s.

INT = Intermediate coloration; Act 2° = active secondary male, with most of the gonad occupied by spermatogenic crypts; Recent 2° = transitional gonad, with much of the gonad still containing degenerating oocytic material, some spermatogenic crypts present; t.s. = tailed sperm present.

ertson, 1972), and its precision has been described on several occasions (e.g., Fricke and Fricke, 1977; Moyer and Nakazono, 1978; Shapiro, 1979, 1980; Ross *et al.*, 1983, 1990; comprehensively reviewed by Ross, 1990). Within the genus *Thalassoma*, social control has been shown in captive groups of *T. lucasanum* (Warner, 1982), and *T. duperrey* (Ross *et al.*, 1983, 1990), but never before under field conditions. In *T. duperrey* it was further shown that it was the relative size of the individual within the local social group that was the cue for sex change; neither the sex nor the coloration of the other individuals in the group appeared to have any additional stimulatory or inhibitive effect. While this is likely to be true for *Thalassoma bifasciatum* as well, it cannot be conclusively shown, given our experimental design.

Shapiro (1980) obtained a remarkably precise response to multiple removals of males in the serranid *Anthias squamipinnis*, and also observed that not all individuals responded immediately to the removal. Instead, sex changes (as indicated by coloration changes) tended to be separated by an interval of about two days. Shapiro hypothesized that the subsequent development of sex change in subordinate females was slowed by the initial development of male characters in higher-ranked females. While our monitoring was not conducted often enough to detect the exact sequence of successive sex changes, some individuals did not initiate the process immediately. Of the 22 individuals that changed sex on the small reefs, 4 were known to have delayed changing at least 7 days after the removal of the males. The aggression directed by large sex-changing females toward other large individuals may have contributed to this delay.

While the removal of TP males in *Thalassoma bifasciatum* results in a precise sex-change response (Fig. 2), it is unclear how this precision is attained. Particularly on bigger reefs with large populations, it seems unlikely that the mechanism is a direct response by one individual to the loss of a particular male. On the basis of their experiments with small groups of fishes, Ross *et al.* (1990) suggested that sex change in *T. duperrey* was mediated by a critical size-ratio mechanism: individuals would change sex when there were sufficiently few larger individuals as well as enough smaller individuals present in the local population. In our study, it is difficult to distinguish direct responses to removal from reactions to changes in the size, sex, or color ratios because removals changed these ratios as well. The proportions of color types in the pre-manipulation populations in our study was variable: from 81 to 96% of the total population was in the IP color phase (Table I). The mean percentage of the total population within the IP size range was 88%, a ratio of IP to TP of 7.3:1. Of the 147 females remaining on all reefs after the initial removals, the 17 largest (11.6%) changed sex, resulting in a color ratio of 7.6:1. One can also investigate the possibility of a critical ratio by mon-

itoring the minimum sex- or size-ratio at which individuals were seen to change sex. In other words, what percent of the population was smaller than the smallest individual seen changing sex on each reef? This varied from 83 to 94%, with a mean of 88.2% ( $n = 5$ ), suggesting a critical ratio of 7.5 smaller individuals to larger. However, we stress that these various ratio measures would be very similar even if a simple one-for-one replacement sex-change mechanism was in operation. To resolve this issue, one would need to vary the number of smaller individuals left on the reef after the male removals, similar to the experiments of Ross *et al.* (1990) for captive populations of *T. duperrey*.

In any event, there is certainly no fixed critical ratio for *T. bifasciatum* as a whole, because the sex and coloration ratios change radically with reef size (Warner and Hoffman, 1980). It may be, however, that individuals respond to a ratio appropriate to the reef on which they find themselves (termed the behavioral-scaling model in Ross, 1990). Sex change of a number of large females also reduces the pool of potential mates for the newly dominant males. If the critical-ratio hypothesis is correct, there should be slightly fewer individuals changing sex than were removed on the experimental reefs. There does exist such a trend in our removal experiments (Fig. 2), but it will take much larger sample sizes to distinguish this trend from random variation.

The behavioral, coloration, and gonadal responses to male removals among the females on the experimental reefs were very rapid, as were seen in other sex-changing species (Robertson, 1972; Shapiro, 1979, 1985). Behavioral responses occurred almost instantaneously, suggesting that the initiation of mating and aggressive behaviors characteristic of males in this species are not dependent on hormone levels (see Crews and Moore, 1986, for a discussion of the various possible relationships between hormones and mating behavior). While we did not collect gametes from matings, it is extremely unlikely that sex-changing individuals could produce sperm in the first few days after the manipulations. Thus these individuals appear capable of spawning in the male role without release of sperm.

Ross (1990) suggested that gametocytes of the heterologous sex are maintained in the gonads of some species to facilitate rapid sex change. While *T. bifasciatum* shows no sign of such heterologous gametocytes in the ovary, this does not appear to inhibit the ability of females to rapidly assume functional male status.

In this study, we could not determine the relative timing of changes in coloration and gonadal condition; all individuals that were collected had initiated changes toward TP coloration, and all were well advanced in sperm production. Stoll (1955) induced both color change and sex change in 13 females with injections of methyl testosterone; the color change began four days after treatment,

and all individuals were producing sperm when they were examined 20 days after the injection. However, other studies on this species have shown that under normal circumstances, sex change can precede color change, because larger IP individuals can be secondary males (Warner and Robertson, 1978).

Individuals should change sex when the reproductive prospects of functioning as the opposite sex exceed the expectations of the current sex (the size-advantage model; see Ghiselin, 1969; Warner *et al.*, 1975; Charnov, 1982a; Warner, 1988b). If mate monopolization depends on the ability to dominate other individuals, and if dominance depends on relative size, then it is the largest individuals in a local population that should change sex in response to large male removals. Relative size does convey dominance in the bluehead wrasse (Warner and Schultz, in prep.), and the largest males are most reproductively successful (Warner, 1984). Accordingly, it is only the largest females that change sex when the TP and INT males are removed (Fig. 1), as predicted by the size-advantage model.

### Acknowledgments

We thank J. Caselle, C. Gabor, and B. L. Rogers for assistance in the field, and E. T. Schultz and two anonymous reviewers for helpful comments. This research was supported by the National Science Foundation (BSR 8704351 to R.R.W.).

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